Paleocene and Miocene *Thyasira* sensu stricto (Bivalvia: Thyasiridae) from chemosynthetic communities from Japan and New Zealand

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ABSTRACT

A new species of bivalve, *Thyasira (Thyasira) beui*, is described from lower to middle Miocene hydrocarbon seep deposits from the North Island of New Zealand. *Thyasira (T.) nakazawai* Matsumoto, 1971 is redescribed from lower Miocene seep deposits in central Honshu of Japan, and *T. (T.)* sp. from Paleocene wood-fall communities in eastern Hokkaido is described as the first *Thyasira* sensu stricto of this age in Japan. As the genus *Conchocele* replaced the niche of *Thyasira* sensu stricto at seep sites from the Eocene in Japan, the occurrence of *T. (T.) nakazawai* is an exceptional occurrence of this genus at younger seeps in Japan. In contrast, *Conchocele* disappeared from New Zealand waters from the end of the Paleocene, leaving *Thyasira* sensu stricto as the sole thyasirid taxon at New Zealand Cenozoic seep sites.

Additional Keywords: Conchocele, Fossil, hydrocarbon seep, cold seep

INTRODUCTION

Bivalves within the family Thyasiridae today inhabit reduced environments from intertidal mudflats to deep-sea hydrothermal vents. Some thyasirid species host chemoautotrophic bacteria in their gills, particularly those toward the larger end of the size range of the family, and some do not (Dufour, 2005; Oliver and Levin, 2006; Taylor and Glover, 2010). Most species within the genus *Thyasira* have two demibranchs and symbionts (Oliver and Killeen, 2002; Dufor, 2005). Such chemosymbiotic thyasirids are deep burrowers and mine sulfide deep in the substrate using their vermiform foot (Dando and Southward, 1986; Seilacher, 1990; Oliver and Killeen, 2002; Dufour and Felbeck, 2003). Thyasirid species can extend their foot up to 30 times the length of the shell (Dufour and Felbeck, 2003).

The oldest known thyasirid, *Cretaxinus hurumi* Hryniewicz, Little, and Nakrem, 2014, comes from uppermost Jurassic to lowermost Cretaceous seeps in Svalbard. As noted by Kiel et al. (2008), *Thyasira rouyana* (d'Orbigny, 1844) from Lower Cretaceous (Valangian–Hauterivian) rocks in Europe is the oldest species of *Thyasira* sensu stricto. By the late Early Cretaceous (Albian), species within this subgenus appeared in seep sites in Hokkaido, northern Japan (Kiel et al., 2008, 2009).

Several species of *Thyasira* sensu stricto have been reported from Cenozoic deposits around the Pacific Rim (Table 1), including *Thyasira* sensu stricto from Paleocene carbonates with plant debris in eastern Hokkaido, Japan, *Thyasira nakazawai* from Miocene accretionary-prism deposits in central Honshu, Japan (Matsumoto, 1971), and *Thyasira* sp. from Miocene seep deposits of North Island, New Zealand (Campbell et al., 2008).

Here we formally describe *Thyasira* sensu stricto fossils from the Paleocene and Miocene of Japan and the Miocene from New Zealand. The descriptions extend knowledge of the fossil species of *Thyasira* sensu stricto

Table 1. Cenozoic *Thyasira* sensu stricto from the Pacific Rim. Symbols: * maximum length (mm); ** length>height; + distinctly longer than high, ± subcircular, – distinctly higher than long; *** medial flattened area.

Species	Country, District	Age	Max L*	L>H**	MF***	Data source
Thyasira (*Thyasira*) sp.	Hokkaido, Japan	Paleocene	10.1	+	–	This study
T. (*T.*) *baca* Devjatilova, 1981	Kamchatka, Russia	Paleocene	13	–	–	Devjatilova and Volobueva (1981)
T. (*T.*) *mironovi* Kalishevich, 1981	South Sakhalin, Russia	Paleocene	12	±	+?	Kalishevich et al. (1981)
T. (*T.*) *uncinata* Kalikevich, 1981	South Sakhalin, Russia	Paleocene	14	+	–	Kalishevich et al. (1981)
T. (*T.*) *xylodia* Kiel and Goedert, 2007	Washington, USA	Latest Eoc.–e. Oligoc.	21	?	–	Kiel and Goedert (2007)
T, (*T.*) *peruviana* Olsson, 1931	Peru	Oligocene	25	±	–	Olsson (1931)
T. (*T.*) *nakazawai* Matsumoto, 1971	central Honshu, Japan	E. Miocene	28.3	+	–	Matsumoto (1971)
T. (*T.*) *minoensis* Itoigawa,1960	central Honshu, Japan	E. Miocene	14.1	–	+	This study
T. (*T.*) *motutaraensis* Powell, 1935	North Is., New Zealand	E. Miocene	6.5	–	–	Powell (1935)
T. (*T.*) *bartrumi* Powell, 1935	North Is., New Zealand	E. Miocene	15	+	+	Powell (1935)
T. (*T.*) *beui* new species	North Is., New Zealand	E.–m. Miocene	13.8	+	–	This study
T. (*T.*) *nana* Khomenko, 1929	Kamchatka, Sakhalin, Russia	M. Miocene	6	+	–	Khomenko (1929)
T. (*T.*) *marwicki* nom. nov.	North Is., New Zealand	L. Miocene	10	+	–	Marwick (1926), as *Thyasira planata*
T. (*T.*) *tokunagai* Kuroda and Habe, 1951	Japan	E. Miocene–rec.	13.6	–	+	This study
T. (*T.*) *gouldii* (Philippi, 1845a)	California, USA	Pliocene–rec.	12	–	+	Oekelmann (1958), Coan et al. (2000)
T. (*T.*) *peregrina* (Iredale, 1930)	New Zealand	Pliocene–rec.	10.4	–	+	This study
T. (*T.*) *ozawai* (Yokoyama, 1926)	Japan	E. Pleistocene	15.3	–	+	This study

in hydrocarbon seep and wood-fall communities from the Pacific Rim.

MATERIALS AND METHODS

The fossils used in this study were collected from two Paleocene sites in Japan and from two Miocene localities in New Zealand. We also examined some Miocene specimens from New Zealand housed at the University of Auckland and one Miocene species described by Matsumoto (1971), which is stored at National Museum of Nature and Science, Tokyo. Details of localities and associated faunas are as follows:

Eastern Hokkaido, Japan. All specimens were collected from two carbonate float blocks from the Katsuhira-zawa (K1) and Katsuhira-kita-zawa (K2) localities of Urahoro Town, eastern Hokkaido, Japan (Figure 1). The upper part of the Katsuhira Formation crops out in this area and consists of mudstones yielding carbonates that contain many plant fragments. The carbonates containing the thyasirid fossils have probably been eroded out from the mudstones of this formation, the age of which has been assigned to the Paleocene (early Selandian) (see Amano and Jenkins, 2014). In addition to the thyasirid bivalves, the carbonates also contain specimens of a provannid(?) gastropod, a limpet, and *Bentharca steffeni* (Amano et al., 2015). The taxonomic composition of this fauna suggests that its primary energy source was the degradation products derived from sunken wood, which was probably bored by xylophagain bivalves.

Central Honshu, Japan. *Thyasira nakazawai* Matsumoto, 1971 was the name proposed for specimens collected from limestone lenses or calcareous mudstones within turbidites of the Wappazawa Formation (Setogawa Group) on a branch of the Hakkou River, 1600 m west of Matsushita, Shimada City (S1) and at Nakadaira, Shimada City (S2) (Figure 1). The age of the Wappazawa Formation has been assigned to the early Miocene (Watanabe, 1988). From the formation, molluscan fossils have been recovered only from the limestone lenses and calcareous mudstones (Matsumoto, 1971). *Thyasira nakazawai* was collected with *Saxolucina* (*Megaxinus*) *matsushitai* Matsumoto, 1971 and *Pitar matsuraensis* (Nagao, 1928) [= *Pliocardia*? sp.]. Based on the fauna and lithofacies of the limestone lenses and calcareous mudstones, the taxa from these localities probably inhabited hydrocarbon seeps.

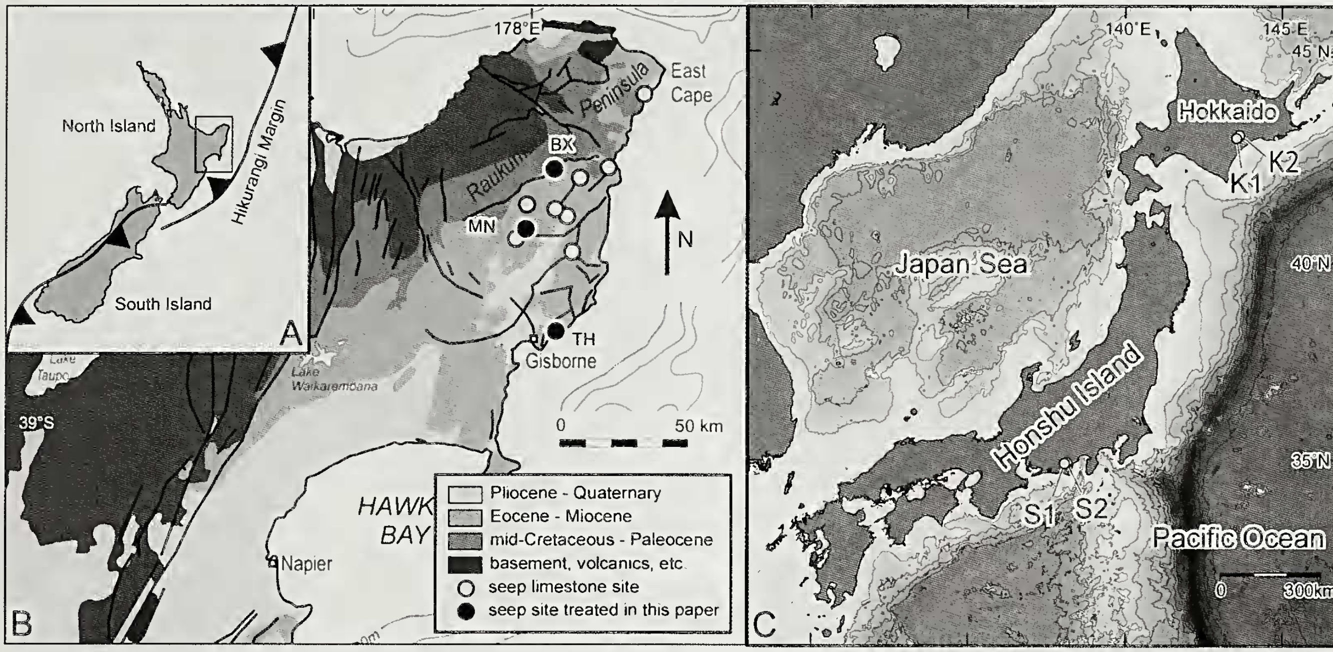


Figure 1. Localities of the fossil *Thyasira* sensu stricto described herein.

North Island, New Zealand. Specimens of *Thyasira beui* new species were collected from hydrocarbon seep carbonates from the Moonlight North (MN), Bexhaven (BX), and Turihaua (TH) localities, north of Gisborne, North Island, New Zealand (Figure 1). The deposits belong to the Bexhaven Limestone, which is assigned to the early to middle Miocene (Campbell et al., 2008). From MN, Amano et al. (2014) described the vesicomyid species *Notocalyptogena neozelandica* and *Pliocardia*? sp. Saether et al. (2010) described the bathymodioline mussels, *Bathymodiolus* (s. l.) *heretaunga*, from BX and MN, and *Gigantidus coseli* from BX, MN, and TH.

We describe the *Thyasira* species in this study using the terminology of Kauffman (1967) and Oliver and Killeen (2002). All figured and supplementary specimens are catalogued at the University of Auckland (UOA L), Joetsu University of Education (JUE) and the National Museum of Nature and Science (NSM).

SYSTEMATIC PALEONTOLOGY

Family Thyasiridae Dall, 1900 (Dall, 1895)
Genus *Thyasira* Lamarck, 1818
Subgenus *Thyasira* Lamarck, 1818

Type Species: *Tellina flexuosa* Montagu, 1803

Remarks: The subgenus *Parathyasira* Iredale, 1930 differs from *Thyasira* sensu stricto by having no shell auricle. Most historical and some recent literature has treated the taxon *Conchocele* as a subgenus of *Thyasira* (e.g., Yabe, H. and S. Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942; Hickman, 1984; Matsui, 1985; Moore, 1988; Matsui, 1990). However, *Conchocele* Gabb, 1866 attains a large size (max. 165.4 mm in length; Kamenev et al., 2001), has a thick shell, and lacks an auricle. Therefore, we regard *Conchocele* as a genus distinct from *Thyasira*.

***Thyasira* (*Thyasira*) *nakazawai* Matsumoto, 1971**
(Figures 2–7)

Thyasira nakazawai Matsumoto, 1971: 665–666, pl. 3, fig. 15–18, Amano, 2014: 7, fig. 1.

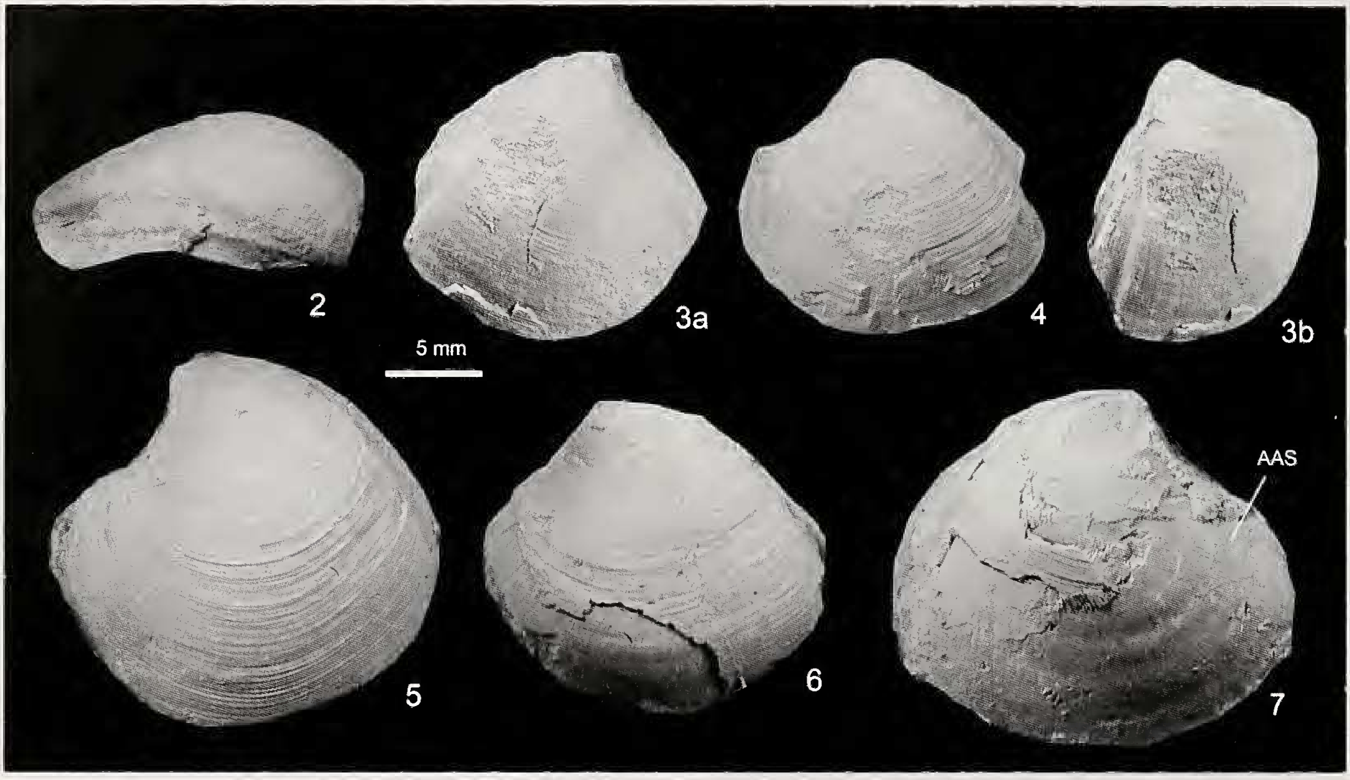
Type Material: Holotype, NSM PM-16922a. Paratypes, NSM PM-16923, NSM PM-16924, NSM PM-16925.

Material Examined: Eleven specimens including the type specimens.

Measurement: See Table 2.

Original Description: “Shell medium in size, thin trigonal oval, nearly long as high, strongly inflated. Antero-dorsal border strongly concave, sharply turned to broadly curved, subangular ventral border forming almost a right angle; postero-dorsal long, faintly arched passing into the ventral border forming an obtuse angle. Beak small, strongly curved forward and situated at about the middle of the shell. Surface of the shell ornamented with fine and concentric, but somewhat irregular growth-lines. Posterior surface depressed from the upper side of the postero-ventral corner making oblique ridge. A central part of the shell faintly ridged from the beak to middle of the ventral border.”

Complementary Description: On examination of the material we found that there are some elements of the



Figures 2–7. *Thyasira (Thyasira) nakazawai* Matsumoto. **2.** Dorsal view of posterior part of left valve; Paratype; NSM PM-16924; Loc. S1. **3a, b.** Frontal and oblique view of right valve; NSM PM-16910; Loc. S2. **4.** Frontal view of left valve; Paratype; NSM PM-16923; Loc. S1. **5.** Frontal view of left valve; Holotype; NSM PM-16922a; Loc. S1. **6.** Frontal view of left valve; NSM PM-16905; Loc. S1. **7.** Inner surface of right valve; AAS, anterior adductor scar; NSM PM-16909; Loc. S1.

Table 2. Measurements of *Thyasira (Thyasira) nakazawai* Matsumoto.

Number of specimens	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve
NSM PM-16922a	Holotype	20.6	19.1	-	0.93	-	left
NSM PM-16923	Paratype	14.9	13.1	-	0.88	-	left
NSM PM-16924	Paratype	15.5+	13.8	-	-	-	left
NSM PM-16925	Paratype	18.5	16.9	-	0.91	-	right
NSM PM-16905		16.2	16.7	-	1.03	-	right
NSM PM-16906		22.0	20.1	15.5	0.91	0.70	both
NSM PM-16908		17.9	17.5	-	0.98	-	left
NSM PM-16909		20.4	17.3	-	0.85	-	right
NSM PM-16910-1		21.0	18.4	-	0.88	-	left
NSM PM-16910-2		16.0	15.5	-	0.97	-	right

original description of the species that are incorrect. We therefore offer here more accurate and complementary morphological information.

Shell rather large for the genus (maximum 28.3 mm in length), thin, ovate, slightly longer than high (height/length ratio = 0.85–0.97; exceptionally 1.03), well inflated (width/length ratio = 0.70). Anterodorsal margin short, strongly concave; anterior margin subcircular and graduating into arched ventral margin. Second posterior fold distinct, but not stronger than first posterior fold; posterior sulcus rather shallow and narrow; first posterior fold strong and ridged; submarginal sulcus distinct; auricle narrow but extending total length of submarginal sulcus. Lunule moderately depressed. Beak prominent, prosogyrate, situated at about one-third of shell length. Shell surface ornamented with fine growth lines. Anterior adductor scar elongate quadrate and attached to pallial line; posterior adductor scar indistinct. Inner surface of shell crenulated by many fine radial lines.

Comparison: *Thyasira (Thyasira) nakazawai* is similar to *T. (T.) tanabei* Kiel, Amano and Jenkins, 2008 from the Upper Cretaceous formations in Hokkaido, sharing a strongly concave anterodorsal margin and strong and ridged posterior fold. However, *T.* (*T.*) *nakazawai* differs from the latter species by having a larger (maximum length of *T.* (*T.*) *tanabei* = 13.5 mm) and more inflated shell with a smaller anterior adductor scar.

Distribution: Lower Miocene Wappazawa Formation of the Setogawa Group from the Shizuoka Prefecture, central Honshu, Japan.

***Thyasira* (*Thyasira*) *beui* new species**
(Figures 8–15)

Thyasira sp.—Campbell et al., 2008: 90.
Thyasira sp. nov.—Saether, 2011: 135–138, fig. 5–19.

Diagnosis: Medium-sized *Thyasira* with suborbicular shell, shallow lunule, and small auricle. Ventral end of first posterior fold occasionally angulated.

Description: Shell up to 13.8 mm in length, rather thin, moderately inflated (width/length ratio = 0.58–0.91), suborbicular (height/length ratio = 0.90–1.17), equivalve and inequilateral. Antero-dorsal margin broadly arched and continuing to rounded anterior margin; ventral margin broadly arched. Auricle small, extending in length two-thirds along marginal sulcus; first posterior fold sharp, with ventral end occasionally angulated; posterior sulcus very shallow; second posterior fold less distinct than first posterior fold. Beak prominent, prosogyrate and located around two-fifths of shell length (i.e., at 36–44% of shell length from anterior margin). Lunule shallow and demarcated by very shallow groove. Shell surface with fine growth lines. Inner shell surface ornamented by many fine radial grooves. Pallial line entire, starting from midpoint of ventral side of anterior adductor scar. Anterior adductor scar elongate-quadrate; posterior adductor scar very small and ovate.

Holotype: UOA L4626 from MN (Y16/f1054), collection AU 15844.

Paratypes: UOA L4627 from MN (Y16/1033), collection AU 19618; UOA L4628 from MN (Y16/f1174), collection AU 19923; UOA L4629 and L4630 from MN (Y16/1059), collection AU 19982; UOA L4631 from BX (Y16/1032), collection AU 19617.

Type Locality: Moonlight North seep carbonates, north of Gisborne, North Island, New Zealand.

Material Examined: Twenty-two specimens from three localities (Loc. MN, BX, TH in Figure 1).

Measurements: See Table 3.

Remarks: *Thyasira* (*Thyasira*) *beui* is *Thyasira* sp. in the compilation of molluscan fossils (in part taken from Beu and Maxwell (1990)) from New Zealand hydrocarbon seep carbonates in Campbell et al. (2008). Saether (2011) described and illustrated this species as "*Thyasira* sp. nov." in his unpublished Ph.D. thesis.

Comparison: *Thyasira* (*Thyasira*) *beui* shares a prominent beak and a moderately inflated shell with *T.* (*T.*) *motutaraensis* Powell, 1935 from the lower Miocene Motutara deposit west of Auckland, North Island, New Zealand (see also Beu and Maxwell, 1990). However, *T.* (*T.*) *motutaraensis* can be separated from the new species by its smaller and higher triangular shell (length = 7.4 mm, height/length ratio = 1.14). *Thyasira* (*T.*) *planata* Marwick, 1926 [this name was preoccupied by Jeffreys, 1882 and a new name, *T.* (*T.*) *marwicki* is proposed herein] from upper Miocene deposits in the western part of North Island, New Zealand, can be distinguished from *T.* (*T.*) *beui* by having a wider posterior area, a longer marginal sulcus, and a narrower auricle than that of the new species. *Thyasira* (*T.*) *mironovi* Kalishevich from the Paleocene of South Sakhalin (Klishevich et al. 1981) is similar to *T.* (*T.*) *beui* in having a first posterior fold with angular ventral end. However, *T.* (*T.*) *mironovi* can be separated from *T.* (*T.*) *beui* by having a less inflated shell, a wider posterior fold and a weak medial flattened area. Another species from the Paleocene of South Sakhalin, *T.* (*T.*) *uncinata* Kalishevich, can be easily distinguished from *T.* (*T.*) *beui* by having an elongate shell with posteriorly situated beak. *Thyasira* (*T.*) *bartrumi* Powell, 1935 from the lower Miocene Motutara deposit is distinctly different from *T.* (*T.*) *beui* by having a *Conchocele*-like shell with beak at anterior one-seventh of shell length and a medial flattened area. The Recent New Zealand species, *T.* (*T.*) *peregrina* Iredale, 1930 differs from *T.* (*T.*) *beui* by its smaller shell (maximum length = 10.4 mm), which is higher than long, and by having a medial flattened area.

Distribution: Lower to middle Miocene Bexhaven Limestone, north of Gisborne, North Island, New Zealand.

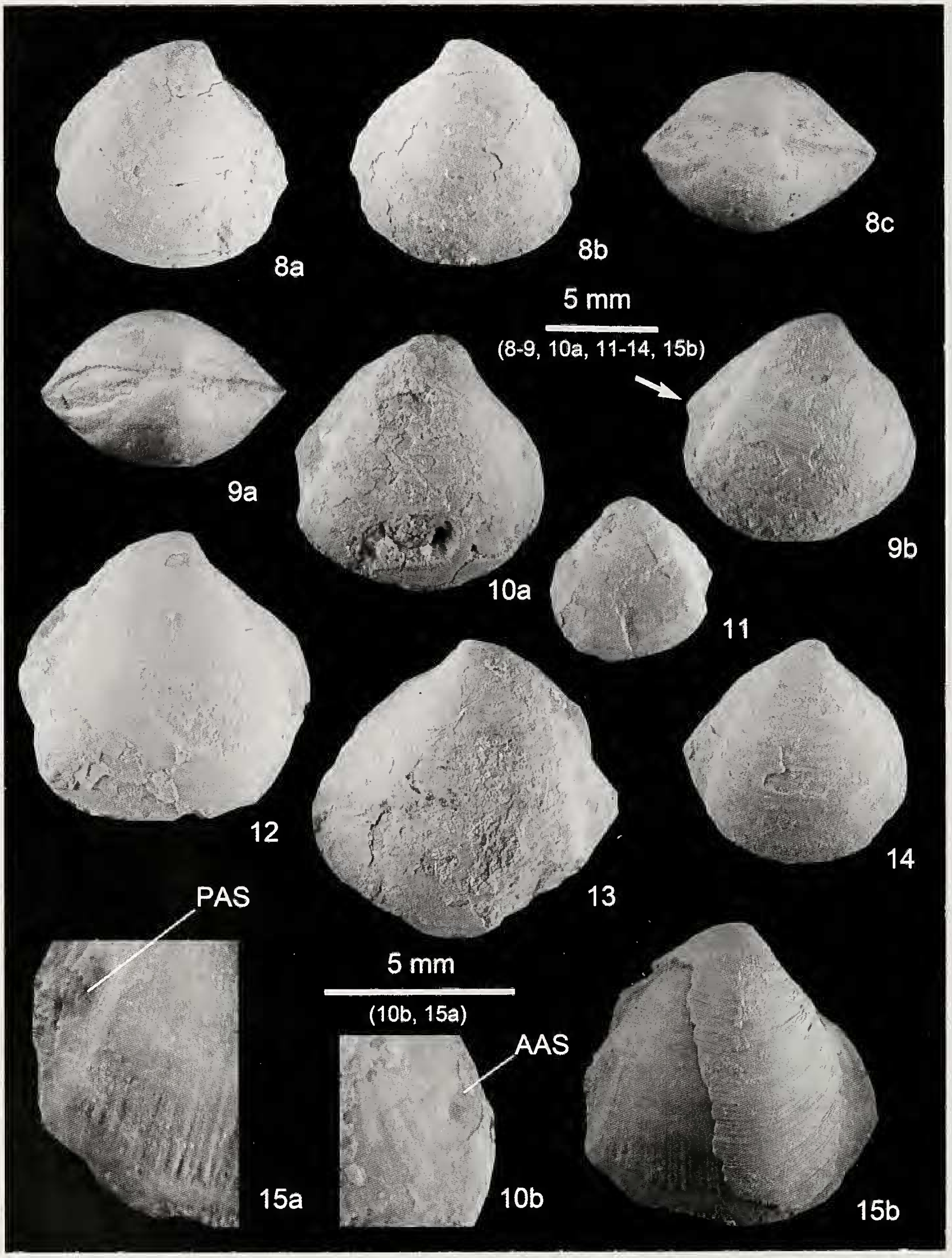
Etymology: Named after Dr. Alan G. Beu who has made significant contributions to the taxonomy of Cenozoic fossil faunas from New Zealand.

***Thyasira* (*Thyasira*) sp.**
(Figures 16–17)

Material Examined: Two articulated but imperfect specimens (JUE nos. 15936, 15937).

Description: Shell rather small in size (9.7–10.1 mm + in length), thin, ovate, longer than high, well inflated (width/length ratio = 0.52–0.58). Anterodorsal margin short, nearly straight; anterior margin subcircular. Second posterior fold distinct; posterior sulcus rather deep; first posterior fold wide and ridged; submarginal sulcus distinct; auricle narrow and short. Beak prosogyrate. Inner structure of shell not preserved.

Comparison: *Thyasira* (*Thyasira*) sp. is similar to the Cretaceous species, *T.* (*T.*) *tanabei* Kiel, Amano and Jenkins, 2008 by having a ridged first posterior fold. However, the wide posterior area of our specimens enables us to separate *T.* (*T.*) sp. from *T.* (*T.*) *tanabei*.



Figures 8–15. ***Thyasira (Thyasira) beui*** **new species**. All specimens except for one illustrated in Figure 15a, b are from the type locality (Moonlight North; MN). One specimen of Figure 15a, b is from Bexhaven (BX). **8a–c.** Frontal and dorsal views of both valves; Paratype, UOA L4629. **9a, b.** Frontal view of right valve and dorsal view of both valves; Holotype; UOA L4626; white arrow showing an angulated ventral end of first posterior fold. **10a, b.** Inner surface of right valve and its enlargement of the area around AAS (= anterior adductor scar); Paratype; UOA L4630. **11.** Frontal view of left valve; Paratype; UOA L4628. **12.** Frontal view of right valve; UOA L4638. **13.** Frontal view of left valve; left valve; UOA L4640. **14.** Frontal view of right valve; UOA L4627. Inner surface of right valve showing PAS (= posterior adduetor scar) and its enlargement; Paratype; UOA L4631.

Table 3. Measurements of *Thyasira* (*Thyasira*) *beui* new species.

Number of specimens	Type	Length (mm)	Height (mm)	Width (mm)	H/L	W/L	Valve	Collection Number	Locality Number
UOA L4626	Holotype	10.2	9.6	6.6	0.94	0.65	both	AU15844	Y16/f1054
UOA L4627	Paratype	10.3	10.2	6.6	0.99	0.64	both	AU19618	Y16/f1033
UOA L4628	Paratype	7.2	7.4	-	1.03	-	left	AU19923	Y16/f1174
UOA L4629	Paratype	9.5	10.4	7.1	1.09	0.75	both	AU19982	Y16/f1059
UOA L4630	Paratype	10.4	10.3	7.0	0.99	0.67	both	AU19982	Y16/f1059
UOA L4631	Paratype	12.4	12.9	9.3	1.04	0.75	both	AU19617	Y16/f1032
UOA L4632		14.8	14.7	10.7	0.99	0.72	both	AU15844	Y16/f1054
UOA L4633		10.5	11.3	7.3	1.08	0.70	both	AU15844	Y16/f1054
UOA L4634		12.7	13.4	9.7	1.06	0.76	both	AU15844	Y16/f1054
UOA L4635		9.2	9.1	-	0.92	-	left	AU19872	Y16/f1048
UOA L4636		11.2	11.0	7.9	0.98	0.71	both	AU19922	Y18/f657
UOA L4637		11.1	10.0	8.0	0.90	0.72	both	AU19922	Y18/f657
UOA L4638		12.9	12.5	-	0.97	-	right	AU19923	Y16/f1174
UOA L4639		9.0	8.1	-	0.90	-	right	AU19923	Y16/f1174
UOA L4640		13.8	12.7	-	0.92	-	left	AU19982	Y16/f1059
UOA L4641		10.7	10.9	7.4	1.02	0.69	both	AU19982	Y16/f1059
UOA L4642		10.2	11.9	9.3	1.17	0.91	both	AU19982	Y16/f1059
UOA L4643		12.0	12.1	7.9	1.01	0.66	both	AU19982	Y16/f1059
UOA L4644		12.6	12.3	9.2	0.98	0.73	both	AU19982	Y16/f1059
UOA L4645		7.6	7.7	4.6	1.01	0.61	both	AU19982	Y16/f1059

T. (*T.*) *xylodia* Kiel and Goedert, 2007 comes from latest Eocene and early Oligocene wood-fall communities in Washington State, USA and can be distinguished from *T.* (*T.*) sp. by its larger size (21 mm in length), deeply concave antero-dorsal margin and narrower posterior area. *T.* (*T.*) *baca* Devjatilova from the Paleocene Getkilninskaya Formation of western Kamchatka (Devjatilova and Volobueva, 1981) differs from *T.* (*T.*) sp. by having a triangular shell and narrower posterior area. *Thyasira* (*T.*) *mironovi* Kalishevich can be distinguished from *T.* (*T.*) sp. by having wider first posterior fold with an angular ventral end and extending its ventral end to the ventral margin of main disc.

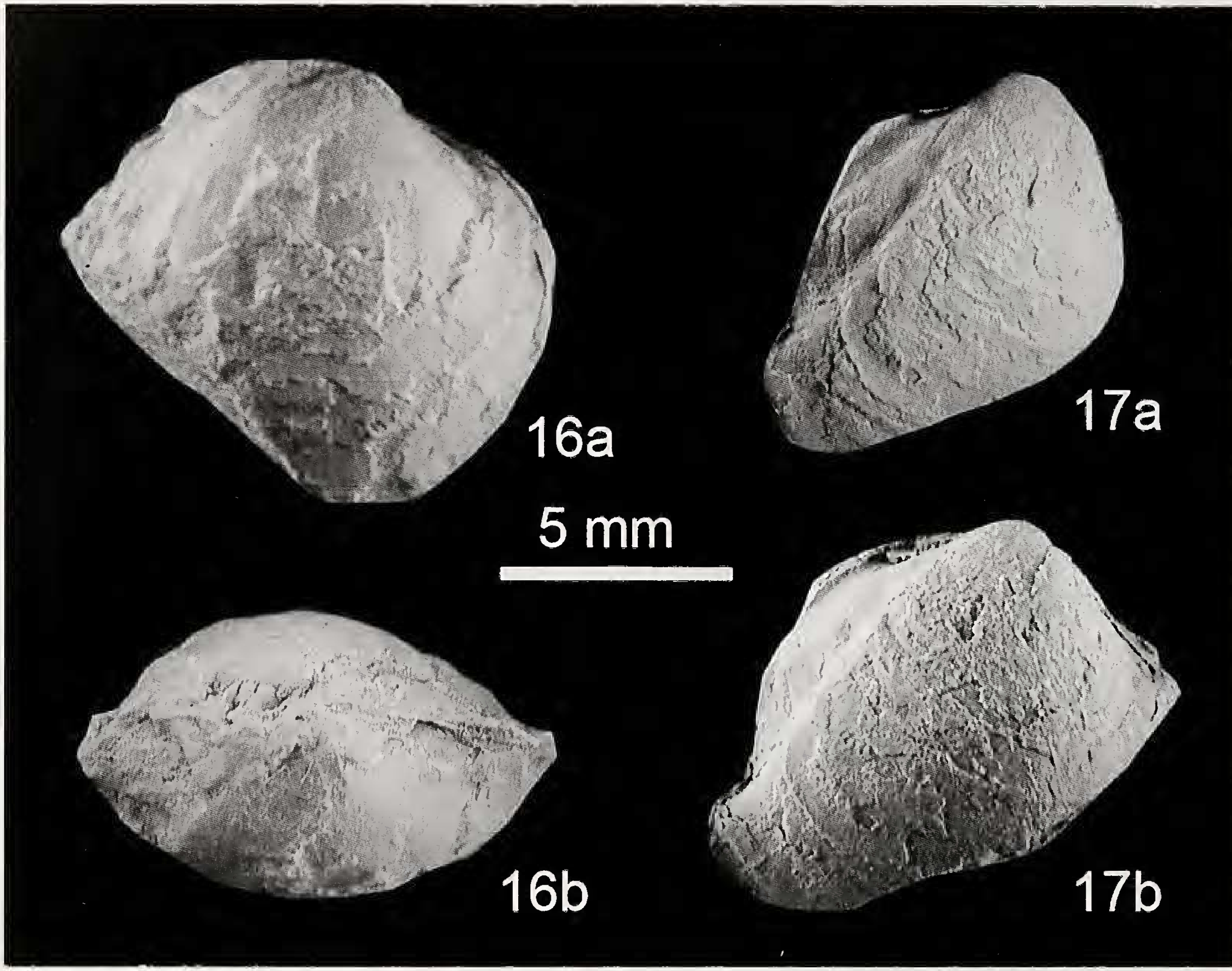
Distribution: Paleocene, upper part of the Katsuhira Formation, eastern Hokkaido, Japan.

DISCUSSION

Several Recent species of *Thyasira* sensu stricto have been recorded from hydrocarbon seep or hydrothermal vent sites (Table 4; Clarke, 1989; Dando et al., 1994; Oliver and Killeen, 2002; Olu et al., 2004; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues et al., 2008). Based on recent molecular analysis of nuclear 18S rRNA and 28S rRNA, the subgenus *Thyasira* sensu stricto is divided into two clades (Taylor et al., 2007). *Thyasira* (*T.*) *sarsi* (Philippi, 1845b) and *T.* (*T.*) *methanophila* Oliver and Sellanes, 2005, from hydrocarbon seeps, form a monophyletic clade. *Thyasira sarsi* itself is an opportunistic species which is also able to live in sediments with low organic content, and at relatively low densities (Keuning et al., 2011). Another clade includes *T.* (*T.*) *flexuosa* (Montagu, 1803), *T.* (*T.*) *gouldii* (Philippi, 1845a), and *T.* (*T.*) *polygonata* (Jeffreys, 1864), none of which have been recorded from seep and vent sites. Morphologically, the *T.* (*T.*) *sarsi*-*T.* (*T.*) *methanophila* clade differs from the *T.* (*T.*) *flexuosa*-*T.* (*T.*) *gouldii*-*T.* (*T.*) *polygonata* clade by having larger (more than 20 mm in length), subcircular or a slightly longer shells, without a medial flattened area. Other *Thyasira* species found in seep and vent sites, such as *T.* (*T.*) *southwardae* Oliver and Holmes, 2006, *T.* (*T.*) *vulcolutre* Rodrigues and Oliver in Rodrigues et al., 2008 and *T.* (*T.*) *oleophila* Clarke, 1989, also have similar shell characteristics to the *T.* (*T.*) *sarsi*-*T.* (*T.*) *methanophila* clade.

Payne and Allen (1991) and Dufour (2005) have shown that in thyasirids demibranch number is related to body size, because asymbiotic thyasirids with only one demibranch only have access to a small amount of nutrients at bathyal depths. All the species discussed above have two demibranchs and chemosynthetic bacteria (Dufour, 2005; Oliver and Sellanes, 2005; Oliver and Holmes, 2006; Rodrigues and Oliver, 2008). Almost certainly because of the abundant supply of hydrogen sulfide at seep and vent sites, thyasirids living there can grow to large sizes relative to thyasirids inhabiting other environments. However, the reason that the thyasirids living in chemosynthetic environments have subcircular or longer shells, without a medial flattened area, is unknown. There are exceptions, as *T.* (*T.*) *striata* (Sturany, 1896), found at a Mediterranean seep by Olu et al. (2004), is characterized by a rather small (ca. 7.5 mm) and higher shell with a medial flattened area. This morphological information from Recent seep and vent *Thyasira* sensu stricto can be used to infer the paleoecology of fossil *Thyasira* sensu stricto species.

As shown in Table 1, *Thyasira* (*T.*) *nakazawai* has a large (length = 28.3 mm) and longer shell (height/length ratio = 0.85–0.97) without a medial flattened area,



Figures 16–17. *Thyasira* (*Thyasira*) sp. **16a, b.** Frontal view of right valve and dorsal view of both valves; JUE no. 15936; Loc. K1. **17a, b.** Frontal and oblique view of right valve; JUE no. 15937; K2.

Table 4. Morphology of recent species of *Thyasira* sensu stricto. * maximum length (mm); ** Length>Height; + distinctly longer than high, ± subcircular, – distinctly higher than long; *** Medial flattened area.

Species	sites	Max L*	L>H**	MF***	Data source
Thyasira (*Thyasira*) *sarsi* (Philippi, 1845b)	seep	25	±	–	Dando et al. (1994), Oliver and Killeen (2002)
T. (*T.*) *methanophila* Oliver and Sellanes, 2005	seep	29.7	+	–	Oliver and Sellanes (2005)
T. (*T.*) *southwardae* Oliver and Holmes, 2006	vent	16.7	+	–	Oliver and Holmes (2006)
T. (*T.*) *vulcolutre* Rodrigues and Oliver, 2008	seep	17.2	±	–	Rodrigues et al. (2008)
T. (*T.*) *oleophila* Clarke, 1989	seep	ca.23	±	–	Clarke (1989)
T. (*T.*) *striata* (Sturany, 1896)	seep	ca.7.5	–	+	Olu et al. (2004)
T. (*T.*) *tokunagai* Kuroda and Habe, 1951	non-seep	13.6	–	+	This study
T. (*T.*) *gouldii* (Philippi, 1845a)	non-seep	12	–	+	Killeen and Oliver (2002b)
T. (*T.*) *polygonata* (Jeffreys, 1864)	non-seep	9	–	+	Killeen and Oliver (2002a)
T. (*T.*) *flexuosa* (Montagu, 1803)	non-seep	12	–	+	Oliver and Killeen (2002)

compared to *Thyasira* sensu stricto species from Cenozoic deposits around the Pacific Rim. Because of this, we speculate that *T.* (*T.*) *nakazawai* might have lived in cold seep areas. In contrast, *T.* (*T.*) *minoensis* Itoigawa, 1960 was collected from non-seep sandstones of the lower Miocene Oidawara Formation; it has a smaller (length = 14.1 mm) and higher shell (height/length ratio = 1.08) and with a distinct medial flattened area.

While the maximum size of *T.* (*T.*) *beui* new species is not large (length = 13.8 mm), the speeies has a suborbicular shell (height/length ratio = 0.90–1.17) without a medial flattened area. The carbonates and associated fauna (see also Campbell et al., 2008) indicate this species also thrived at fossil seep sites. Judging from the lithofacies and the associated fauna of limpets and provannids, the Paleocene *T.* (*T.*) sp. collected from eastern Hokkaido might have been a member of a fossil wood-fall community. Despite the small size of *T.* (*T.*) sp. (length = 9.7–10.1 mm) compared with other seep species, it also is longer than high and has no medial flattened area. Such small thyasirid species also have been recognized in Late Cretaceous wood-fall communities with limpets and provannids by Kiel et al. (2009). In the northern Pacific area, *Thyasira* sensu stricto occurred in hydrocarbon seeps and wood-fall sites during the Late Cretaceous (Kiel et al., 2008, 2009). The eastern Hokkaido Paleocene *Thyasira* sensu stricto species might have lived in wood-fall communities. The first large thyasirid, *Thyasira townsendi* (White, 1890) (almost certainly a species of *Conchocele*) appeared in Maastrichtian seep deposits of Snow Hill Island, Antarctica (Kiel et al., 2008; Little et al. 2015). The second oldest large thyasirid species, *Conchocele* aff. *conradi* (Rosenkrantz, 1942), is from the Danian Kangilia Formation of western Greenland (Rosenkrantz, 1970; Amano, 2014). From North Island, New Zealand, one specimen of *Conchocele* sp. has been recorded from Paleocene deposits at Angora Road, south of Wimbledon (Beu and Maxwell, 1990; Beu, 2014 personal communication). Another Paleocene *Conchocele* speeimen up to 70 mm in length was collected from 1 km south of Te Kaukau Point, White Rock, South Wairarapa coast (Beu, 2014 personal communication). So far, no fossil *Conchocele* has been recorded from Paleocene deposits in the northern Pacific area.

Since the Eocene, the genus *Conchocele* seems to have replaced the niche of *Thyasira* sensu stricto in the northern Pacific. Lots of literature has described the radiation of *Conchocele* in Eocene to Recent times in this region (e.g., Yabe and Nomura, 1925; Grant and Gale, 1931; Krishtofovich, 1936; Slodkewitsch, 1938; Weaver, 1942; Hickman, 1984; Moore, 1988; Kamenev et al., 2001). *Conchocele* was also found from Eocene to Holocene seep sites and in Oligocene to Miocene whale-fall sites (Goedert et al., 1995; Majima et al., 2005; Amano et al., 2007; Kiel and Goedert, 2006). Thus the occurrence of *Thyasira* (*Thyasira*) *nakazawai* from lower Miocene seep deposits is an exceptional post-Eocene occurrence of *Thyasira* (*Thyasira*) species in the northern Pacific area. In contrast, in New Zealand *T.* (*T.*) *beui* occurs in lower to middle Miocene seep sites, in the absence of *Conchocele* from the region.

Conchocele might have migrated from western Greenland to the northern Pacific area (including Japan) by the Eocene (Amano and Jenkins, 2014), and once there to have replaced *Thyasira* sensu stricto because of its tolerance to lower oxygen environments. In New Zealand waters, in contrast, *Conchocele* did not invade hydrocarbon seep sites and had disappeared from the region by end of the Paleocene. Thyasirids (probably *Thyasira* sensu stricto) from New Zealand Cretaceous seep deposits (Kiel et al., 2013) show that small sized thyasirids have flourished in the area since that time period.

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